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Taxonomic Accounts and Phylogenetic Positions of the Far East Asian Centipedes *Scolopocryptops elegans* and *S. curtus* (Chilopoda: Scolopendromorpha)

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The epigean centipede genus *Scolopocryptops* Newport, 1844 consists of two monophyletic lineages, the “Asian/North American” and “Neotropical/Afrotropical” groups. Most of the “Asian/North American” species bear the complete sulcus/sulci along the lateral margin of the cephalic plate and sternites lacking sulci, whereas Japanese *Scolopocryptops elegans* (Takakuwa, 1937) bears short lateral sulci on the cephalic plate and Taiwanese *Scolopocryptops curtus* (Takakuwa, 1939) lacks the cephalic marginal sulci, and both species bear a longitudinal sternal sulcus. The taxonomic accounts of *S. elegans* and *S. curtus* were revisited in this study based on newly collected specimens. We found that these two species share a characteristic of the second maxilla, that they lack the transparent margin on the dorsal brush, which distinguishes them from other “Asian/North American” species. *Scolopocryptops elegans* and *S. curtus* can be distinguished from each other by the characters of their antennal articles, cephalic plate, forcipular coxosternite, tergite 23, and coxopleuron. Phylogenetic analyses using nuclear 28S ribosomal RNA and mitochondrial cytochrome c oxidase subunit I sequences confirmed that *S. elegans* and *S. curtus* are closely related and form a single clade sister to a clade comprising all the other “Asian/North American” *Scolopocryptops* species.

Key words: Japanese Archipelago, molecular phylogeny, Ryukyu Islands, Taiwan, second maxilla

INTRODUCTION

Blind epigean centipedes of the genus *Scolopocryptops* Newport, 1844 are widely distributed in the New World, West Africa, and the islands and continental area along the eastern to southern Pacific Rim from Japan to New Guinea and Fiji (Edgecombe and Bonato, 2011; Schileyko et al., 2020). *Scolopocryptops* currently comprises 27 species, mostly described from North and South America and East Asia (Schileyko et al., 2020; Xiao et al., 2021). The thus-far known Japanese *Scolopocryptops* comprise eight species, and six from the Japanese Archipelago have been described to date. Molecular phylogenetic analysis has shown that the genus consists of two major clades, the “Asian/North American” and “Neotropical/Afrotropical” groups (Edgecombe et al., 2012; Vahtera et al., 2013); however, the species-level phylogenetic relationships of *Scolopocryptops* species remain unclear because of a lack of sequence data.

Most of the Asian and North American *Scolopocryptops*, including the species indigenous to the Japanese Archipelago, bear the complete marginal sulcus/sulci along the lateral margin of the cephalic plate and sternites lacking sulci/sutures (e.g., Takakuwa, 1940; Shinohara, 1984, 1990; Shelly, 2002). By contrast, two species described from Japan and Taiwan, *Scolopocryptops elegans* (Takakuwa,

1937) and *Scolopocryptops curtus* (Takakuwa, 1939), share several features that distinguish them from most other “Asian/North American” species: *S. elegans* bears short sulci along the lateral margin of the cephalic plate and *S. curtus* lacks the cephalic marginal sulci, and both of them bear a longitudinal sulcus on the sternites (for *S. elegans*, Takakuwa [1937, 1940], and for *S. curtus*, Takakuwa [1939, 1940] and Chao and Chang [2008]).

Scolopocryptops elegans was described based on multiple specimens from Katsurahama, Kochi Prefecture (Takakuwa, 1937). This species is widely recorded in Japan, ranging from northeastern Honshu of the Japanese Archipelago to the Ryukyu Islands (Shinohara, 1950; Ômine et al., 1982). *Scolopocryptops curtus* was described from Hengchun Township in Pingtung County, Taiwan (Takakuwa, 1939), and is also recorded from southern Kyushu and Ryukyu Islands (Ogawa, 1961; Ômine, 1969; Ômine and Ito, 1998). Although the detailed morphological features of *S. elegans* and *S. curtus* were not characterized in the original descriptions (Takakuwa, 1937, 1939), *S. curtus* was re-described based on newly collected materials by Chao and Chang (2008). In this study, we provide a redescription of *S. elegans* based on specimens newly collected from the type locality and several locations in Japan. The detailed morphology of *S. curtus* was also reexamined to clarify the relationships between *S. elegans* and *S. curtus*. The phylogenetic relationships of *S. elegans* and *S. curtus* with other members of the “Asian/North American” species group were

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estimated using nuclear and mitochondrial DNA sequences to clarify whether these two species form a clade within the “Asian/North American” group.

MATERIALS AND METHODS

Taxon sampling and morphological examination

Specimens of *S. elegans* were collected from the type locality, Katsurahama, Kochi Prefecture, Japan, under fallen leaves and rotten trees in a laurel forest, as well as from additional localities in Honshu and Shikoku, Japan (Figs. 1, 2A). Specimens of *S. curtus* were obtained from several localities on Iriomote Island, Ryukyu

Islands, Japan, and Taiwan (Fig. 1). Additionally, three Japanese *Scolopocryptops* species were collected from their type localities for molecular analyses: *S. quadristriatus* (Verhoeff, 1934) from Tokyo, Honshu on 15 April 2017; *S. ogawai* Shinohara, 1984 from Shizuoka Prefecture, Honshu (34.739659°N, 137.977503°E) on 22 March 2021; and *S. musashiensis* Shinohara, 1984 from Chiba Prefecture, Honshu (35.751703°N, 139.900238°E) on 20 October 2021. Additionally, *S. rubiginosus* (L. Koch, 1878), whose type locality is stated as “Japan” (Koch, 1878), was obtained from Kanagawa Prefecture, Honshu (35.298592°N, 139.477019°E) on 18 October 2021.

Specimens were fixed in 70% or 99% ethanol after they had

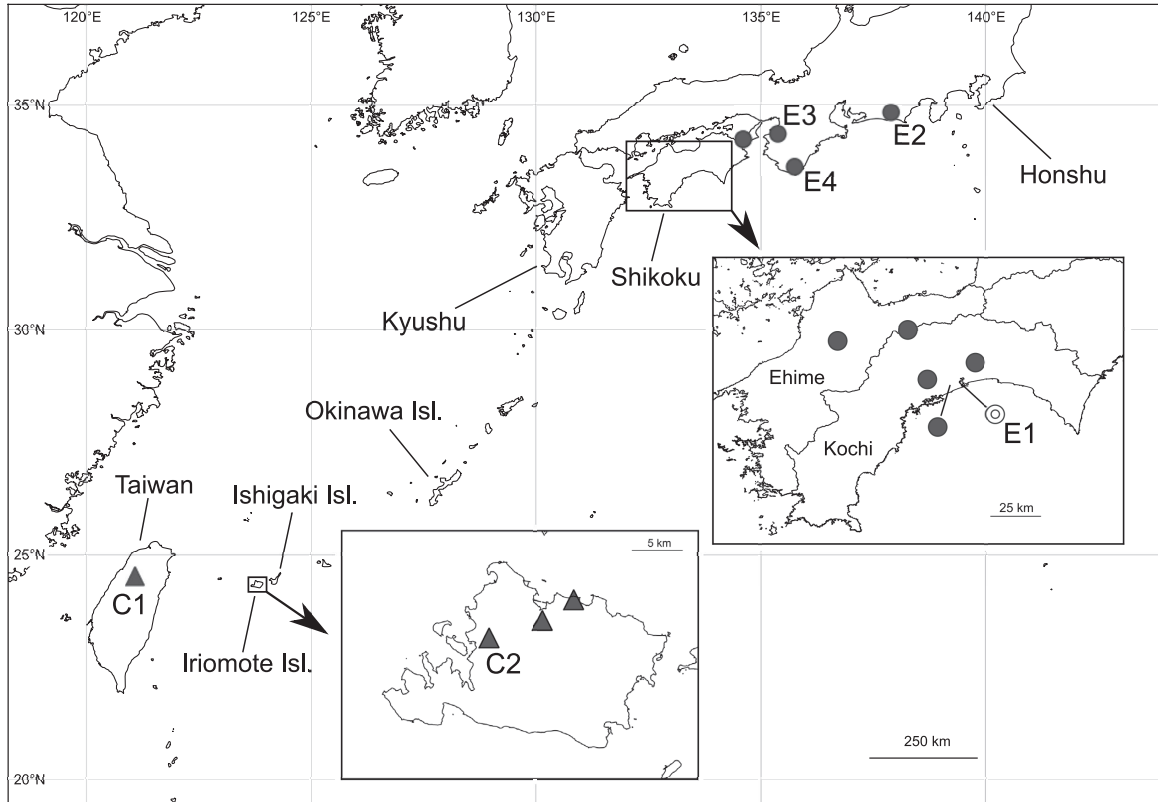


Fig. 1. Map showing the collection localities of *Scolopocryptops elegans* (Takakuwa, 1937) and *S. curtus* (Takakuwa, 1939) in the present study. The double circle denotes the type locality of *S. elegans*, and filled circles denote non-type localities of *S. elegans*; triangles show the collection localities of *S. curtus*. Locality numbers (E1–E4, C1, and C2) are shown in Fig. 10 and Table 1.

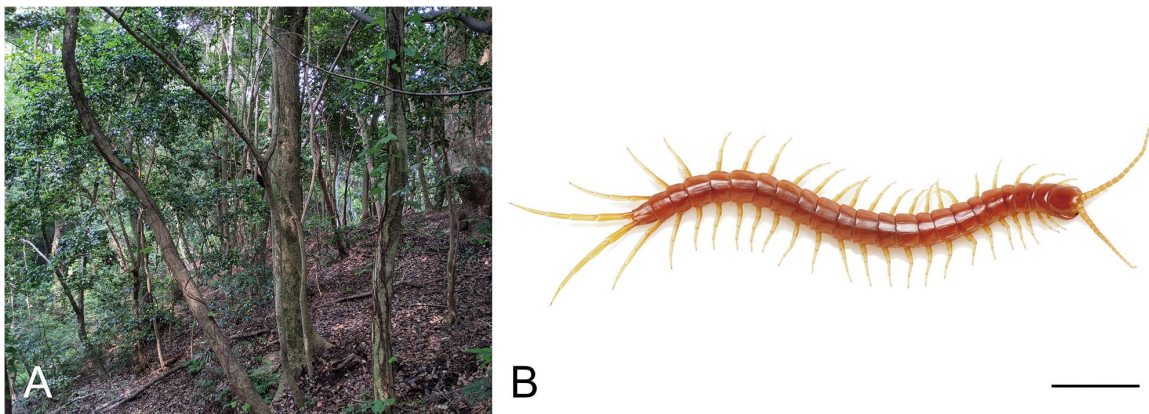


Fig. 2. *Scolopocryptops elegans* (Takakuwa, 1937), from near the type locality, KUZ Z4066, and habitat at the type locality. (A) Habitat (laurel tree forest) at Katsurahama, Kochi Prefecture. (B) Live specimen, dorsal view. Scale bar: 10 mm.

been placed in 30% ethanol for a while, and then preserved in 70% ethanol. Leg-bearing segment 23 was dissected in several specimens to examine genital morphology. All the specimens were examined using a Leica M125C stereoscopic microscope with a drawing tube (Leica Microsystems, Wetzlar, Germany). The specimens were photographed using a Sony a6500 digital camera and a 65 mm macro lens, or a Leica MC170 HD digital camera on the Leica M125C. Images captured with the Leica MC170 were processed using the software Leica Application Suite v. 4.1.2. Specimens examined are deposited in the Zoological Collection of Kyoto University (KUZ).

The terminology for external morphology followed Lewis et al. (2005) and Bonato et al. (2010). Growth stadium (juvenile, subadult, or adult) was determined based on the body length and development of genital segments. For dissected adults and individuals with everted genital organs, sex was determined by using the data of Takakuwa (1933); the terminology for genital organs followed Demange and Richard (1969) and Iorio (2003).

Also, part of Takakuwa's myriapod collection (see Jonishi and Nakano, 2022) was investigated to clarify whether the remnants of his collection contained the type series of *S. elegans* and *S. curtus*.

DNA extraction, PCR, and DNA sequencing

Total DNA was extracted from leg samples using a DNA Blood and Tissue Kit (Qiagen, Hilden, Germany) or a NucleoSpin Tissue kit (Macherey-Nagel, Duren, Germany). Phylogenetic analyses were conducted using nuclear 28S rRNA (28S) and mitochondrial cytochrome *c* oxidase subunit I (COI) markers following previous

studies (Vahtera et al., 2012, 2013). The 28S fragment was amplified using the primer pair 28Sa/28Sb (Whiting et al., 1997), and the COI fragment was amplified using the primers LCO1490/HCOout-out (Folmer et al., 1994; Schwendinger and Giribet, 2005). Each PCR was performed using TaKaRa Ex Taq DNA polymerase or TaKaRa Ex Premier DNA Polymerase (Takara Bio Inc., Shiga, Japan). For 28S and COI, reactions were performed using a GeneAmp PCR System 9700 (Thermo Fisher Scientific, Waltham, USA) and a T-100 Thermal Cycler (Bio-Rad, Hercules, USA) respectively. The PCR mixtures were heated to 94°C for 5 min, followed by 35 cycles at 94°C (10 s), 60°C for 28S, or 50°C for COI (20 s), and then 72°C (30 s for 28S and 42–48 s for COI), with a final extension at 72°C for 6 min. The cycle sequencing reactions were conducted using a SupreDye Cycle Sequencing Kit (M&S Techno Systems, Osaka, Japan). Each cycle sequencing mixture was heated to 96°C (2 min), followed by 40 cycles of 96°C (10 s), 50°C (5 s), and then 60°C (48 s). The cycle-sequencing products were collected by ethanol precipitation and sequenced on an ABI 3130xl Genetic Analyzer (Thermo Fisher Scientific). Chromatograms were visualized and assembled using the software DNA BASER (Heracle Bio-soft S. R. L., Arges, Romania). In total, 20 sequences were obtained, and deposited in the International Nucleotide Sequence Databases (INSD) through the DNA Data Bank of Japan (Table 1).

Molecular phylogenetic analyses

A total of 24 sequences of Scolopocryptopidae were obtained from INSD (Table 1) from eight species of the "Asian/North American" group, i.e., *S. capillipedatus* Takakuwa, 1938, *S. curtus*,

Table 1. Samples used for the molecular analyses. The information on the voucher is accompanied by the collection locality and the INSD accession numbers of the DNA sequences. Locality numbers are shown in Fig. 1 and Fig. 10. Acronyms: AMNH, American Museum of Natural History; CMMI, Institute of Chinese Materia Medica, China Academy of Chinese Medical Sciences; KUZ, Zoological Collection of Kyoto University; MCZ, Museum of Comparative Zoology, Harvard University; and SYSU, National Sun Yat-sen University.

Species	Voucher #	Locality	Locality #	INSD #		References
				28S	COI	
Scolopocryptops						
<i>Scolopocryptops capillipedatus</i>	SYSU Chilo-044	Yanping, Taitung, Taiwan	—	—	AB617528	Chao et al. (unpublished)
<i>Scolopocryptops capillipedatus</i>	SYSU Chilo-056	Heping, Taichung, Taiwan	—	—	AB617529	Chao et al. (unpublished)
<i>Scolopocryptops capillipedatus</i>	SYSU Chilo-061	Datong, Yilan, Taiwan	—	—	AB617530	Chao et al. (unpublished)
<i>Scolopocryptops capillipedatus</i>	SYSU Chilo-143	Taoyuan, Kaohsiung, Taiwan	—	—	AB672646	Chao et al. (unpublished)
<i>Scolopocryptops curtus</i>	SYSU Chilo-025	Beitou, Taipei, Taiwan	—	—	AB617531	Chao et al. (unpublished)
<i>Scolopocryptops curtus</i>	SYSU Chilo-045	Yanping, Taitung, Taiwan	—	—	AB617532	Chao et al. (unpublished)
<i>Scolopocryptops curtus</i>	KUZ Z4079	Tai'an, Miaoli, Taiwan	C1	LC700502	LC700501	This study
<i>Scolopocryptops curtus</i>	KUZ Z4081	Iriomote Island, Okinawa, Japan	C2	LC700504	LC700503	This study
<i>Scolopocryptops elegans</i>	KUZ Z4062	Katsurahama, Kochi, Japan	E1	LC700494	LC700493	This study
<i>Scolopocryptops elegans</i>	KUZ Z4068	Fukuroi, Shizuoka, Japan	E2	LC700496	LC700495	This study
<i>Scolopocryptops elegans</i>	KUZ Z4071	Kinokawa, Wakayama, Japan	E3	LC700498	LC700497	This study
<i>Scolopocryptops elegans</i>	KUZ Z4073	Higashimuro, Wakayama, Japan	E4	LC700500	LC700499	This study
" <i>Scolopocryptops mexicanus</i> "	MCZ IZ-130812	Napo, Ecuador	—	JX422593	JX422679	Edgecombe et al. (2012)
<i>Scolopocryptops musashiensis</i>	KUZ Z4085	Ichikawa, Chiba, Japan	—	LC700512	LC700511	This study
<i>Scolopocryptops nigridius</i>	MCZ IZ-130806	North Carolina, USA	—	JX422594	JX422680	Edgecombe et al. (2012)
<i>Scolopocryptops nigridius</i>	MCZ DNA100807	North Carolina, USA	—	HM453278	AY288744	Vahtera et al. (2012) for 28S; Edgecombe and Giribet (2004) for COI
<i>Scolopocryptops nigrimaculatus</i>	CMMI 20181207002	Hangzhou, China	—	—	MT093844	Jiang et al. (2020)
" <i>Scolopocryptops nipponicus</i> "	MCZ IZ-130804	Nagoya, Aichi, Japan	—	JX422595	JX422681	Edgecombe et al. (2012)
<i>Scolopocryptops ogawai</i>	KUZ Z4084	Fukuroi, Shizuoka, Japan	—	LC700510	LC700509	This study
<i>Scolopocryptops quadristriatus</i>	KUZ Z4083	Urataka-cho, Hachioji, Tokyo, Japan	—	LC700508	LC700507	This study
<i>Scolopocryptops rubiginosus</i>	SYSU Chilo-113	Tam Dao, Vinh Phuc, Vietnam	—	—	AB672647	Chao et al. (unpublished)
<i>Scolopocryptops rubiginosus</i>	SYSU Chilo-105	Chengdu, Sichuan, China	—	—	AB672648	Chao et al. (unpublished)
<i>Scolopocryptops rubiginosus</i>	SYSU Chilo-036	Liouguei, Kaohsiung, Taiwan	—	—	AB672649	Chao et al. (unpublished)
<i>Scolopocryptops rubiginosus</i>	KUZ Z4082	Enoshima, Kanagawa, Japan	—	LC700506	LC700505	This study
<i>Scolopocryptops sexspinosus</i>	MCZ IZ-131450	North Carolina, USA	—	AY288710	AY288745	Edgecombe and Giribet (2004)
<i>Scolopocryptops spinicaudus</i>	AMNH IZC 00146514	California, USA	—	JX422596	JX422683	Edgecombe et al. (2012)
Outgroup						
<i>Newportia monticola</i>	MCZ IZ-130777	Parque de Cahuita, Costa Rica	—	KF676360	KF676507	Vahtera et al. (2013)

S. nigridius McNeil, 1887, *S. nigrimaculatus* Song et al., 2004, “*S. nipponicus*” Shinohara, 1990 sensu Edgecombe et al. (2012) (= *S. spinicaudus* Wood, 1862; see Shelly, 2002), *S. rubiginosus*, *S. sexspinosus* (Say, 1821), and *S. spinicaudus*, and the “Neotropical/Afrotropical” nominal species “*S. mexicanus*” Humbert and Saussure, 1869 sensu Edgecombe et al. (2012) (= *S. ferrugineus* (Linnaeus, 1767); see Attems, 1930); *Newportia monticola* Pocock, 1890 was used as an outgroup taxon.

The nuclear 28S sequences were aligned using MAFFT Q-INS-i (Kuraku et al., 2013; Katoh et al., 2019) considering the RNA secondary structure information, and non-conserved regions were trimmed using Gblocks (Castresana, 2000). Alignment of the mitochondrial COI was trivial because no indels were observed. The aligned sequences of 28S and COI were 478 and 658 bp, respectively. Because the first four positions of COI were missing in most of the sequences, this portion of the COI sequences were excluded from the analyses. Therefore, the concatenated sequence yielded 1132 bp of aligned positions.

Phylogenetic trees were reconstructed using maximum likelihood (ML) and Bayesian Inference (BI). The best-fit partition scheme and models were identified based on the Bayesian information criterion (BIC) using PartitionFinder v. 2.1.1 (Lanfear et al., 2017) with the “all” algorithm. The selected partition scheme and models were as follows: TRNEF + G or GTR + G for 28S, TRNEF + G or SYM + G for COI 1st position, F81 + I for COI 2nd position, and TRN + G or GTR + G for COI 3rd position. The ML phylogenetic tree was inferred using IQ-TREE v. 1.6.12 (Nguyen et al., 2015) with non-parametric bootstrapping (BS) conducted with 1000 replicates. BI tree and Bayesian posterior probabilities (BPP) were estimated using MrBayes v. 3.2.7 (Ronquist et al., 2012). Two independent

runs of four Markov chains were conducted for 1 million generations, and the tree was sampled every 100 generations. According to parameter estimates and assessment of convergence using Tracer v. 1.7.2 (Rambaut et al., 2018), the first 4441 trees were discarded. Uncorrected pairwise distances for COI sequences (614–654 bp) were calculated using MEGA X (Kumar et al., 2018).

Because *S. elegans* showed non-monophyletic relationships in the unconstrained tree, the approximately unbiased (AU) test (Shimodaira, 2002) was performed based on the ML tree with IQ-TREE, to test whether the best tree possible under the constraint of *S. elegans* monophyly was a significantly worse fit to the data than the best tree without this constraint.

RESULTS

Taxonomy

Genus *Scolopocryptops* Newport, 1844

[Japanese name: Akamukade-zoku]

Scolopocryptops elegans (Takakuwa, 1937)

[Japanese name: Ke-akamukade]

(Figs. 2–5)

Otocryptops elegans Takakuwa, 1937, pp. 203–205, figs. 1, 2; Takakuwa, 1940, pp. 73–74, fig. 78.

Scolopocryptops elegans: Shinohara, 1978, p. 3; Shinohara et al., 2015, pp. 880, 905.

Amended diagnosis. Antenna with sparse minute hairs

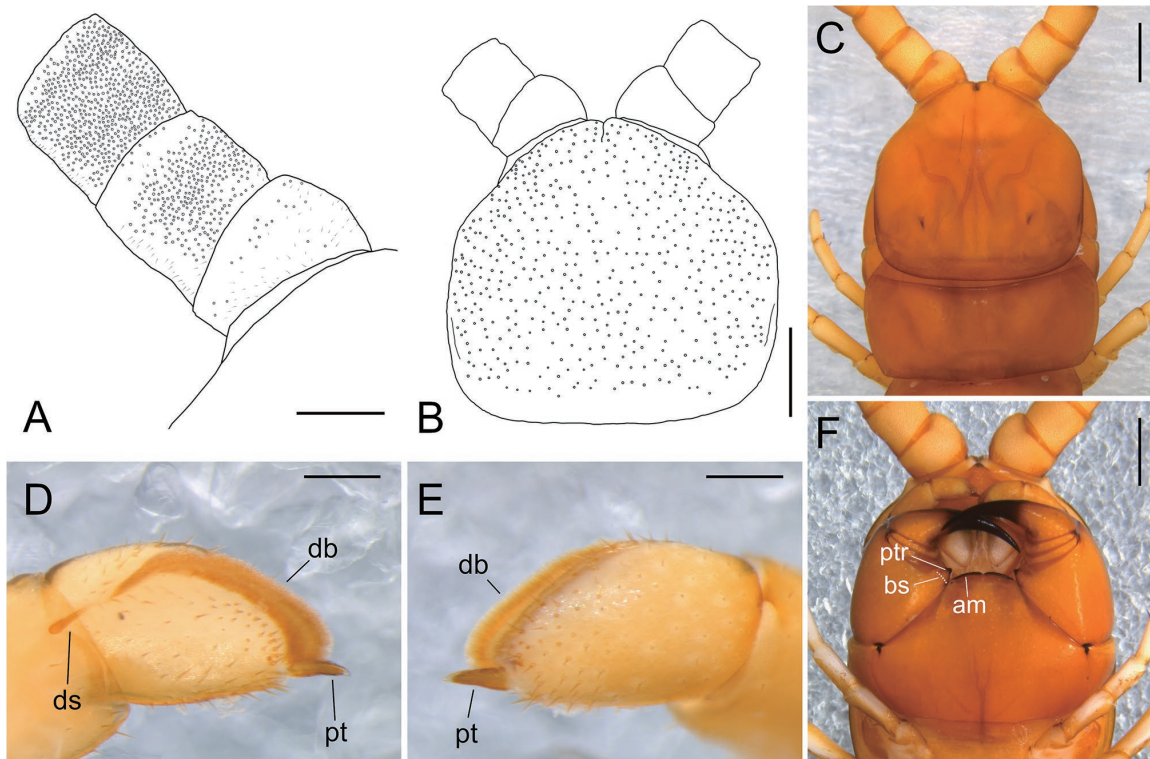


Fig. 3. *Scolopocryptops elegans* (Takakuwa, 1937), from near the type locality, KUZ Z4064 (A–C, F) and KUZ Z4067 (D, E). (A) Left antenna, dorsal view. (B) Cephalic plate, dorsal view. (C) Cephalic plate and tergite 1, dorsal view. (D) Distal part of article 2, article 3, and pretarsus of left second maxilla, medial view. (E) Article 3 and pretarsus of left second maxilla, lateral view. (F) Head, ventral view. Abbreviations: am, anterior margin of forcipular coxosternite; bs, basal suture on trochanteroprefemoral process; db, dorsal brush on article 3 of second maxilla; ds, dorsal spur on article 2 of second maxilla; pt, pretarsus of second maxilla; ptr, process of forcipular trochanteroprefemur. Scale bars: 0.5 mm (A), 1 mm (B, C, F), 0.2 mm (D, E).

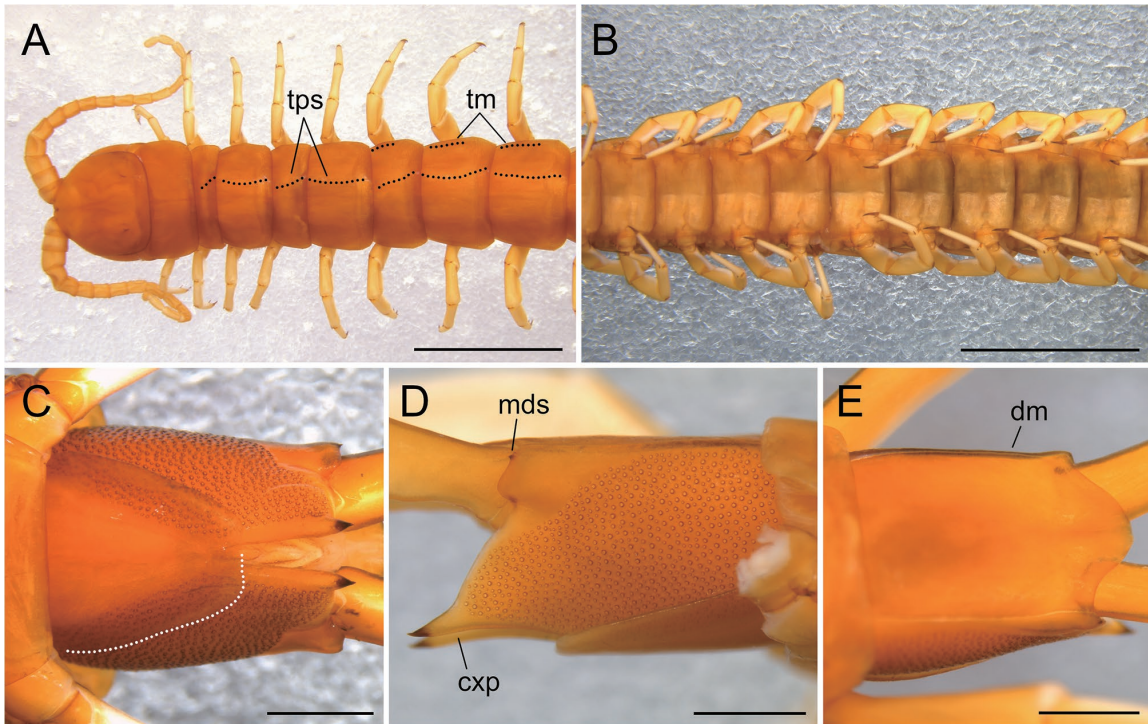


Fig. 4. *Scolopocryptops elegans* (Takakuwa, 1937), from the type locality and its adjacent locations, KUZ Z4061 (B), KUZ Z4064 (C, E), KUZ Z4066 (A), and KUZ Z4067 (D). (A) Cephalic plate and tergites 1–8, dorsal view; dashed lines denote right tergal paramedian sutures and marginations. (B) Sternites 8–16, ventral view. (C) Sternite 23, ventral view. Dashed line indicates its right margin. (D) Right coxopleuron, lateral view. (E) Tergite 23, dorso-lateral view. Abbreviations: cxp, coxopleural process; dm, dorsal margin of ultimate pleuron; mds, minute dark spine on ultimate pleuron; tm, tergal margination; tps, tergal paramedian suture. Scale bars: 5 mm (A, B), 1 mm (C–E).

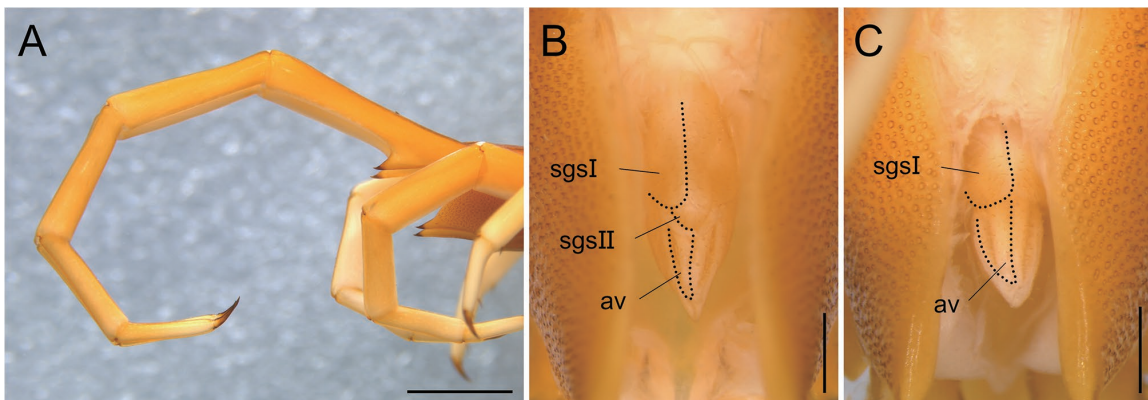


Fig. 5. *Scolopocryptops elegans* (Takakuwa, 1937), from near the type locality, KUZ Z4065 (C), KUZ Z4066 (A), and KUZ Z4067 (B). (A) Right ultimate leg, lateral view. (B) Male genital segments and anal valves, ventral view. (C) Female genital segment and anal valves, ventral view. Abbreviations: av, anal valve; sgs I, sternite of genital segment 1; sgs II, sternite of genital segment 2. Scale bars: 2 mm (A), 0.5 mm (B, C).

and short setae on dorsal surface of basalmost article, subsequent articles densely covered with setae. Cephalic plate with short lateral marginal sulci in posterior half. Forcipular coxosternite with anterior margin weakly convex and bilobed. Sternites 2–20 with shallow longitudinal sulcus and transverse depression. Coxopleuron approx. 1.5–1.7× as long as sternite 23, pleural dorsal margin protruding from lateral margin of tergite 23, posterior and ventral margins forming approx. 60–65° angle; coxopleural process moderately long.

Material examined. *Specimens from the type locality*

and adjacent areas. Japan: three subadults, Shikoku, Kochi, Katsurahama (type locality; 33.497192°N, 133.572684°E; elev. 37.4 m), 23 June 2021, leg. TJ and Taiga Kato (TK), KUZ Z4061–Z4063; one male, Kochi, Haruno-cho (33.514447°N, 133.498778°E; elev. 26.4 m), 23 June 2021, leg. TJ, KUZ Z4064; one female, Kochi, Hidaka, near Saruda-do Cave (33.515308°N, 133.356779°E; elev. 60.8 m), 24 June 2021, leg. TK, KUZ Z4065; one male, Kochi, Nankoku, Yakyo (33.61358°N, 133.621666°E; elev. 92.4 m), 25 June 2021, leg. TJ, KUZ Z4066; one male, Kochi, Nankoku, Shirakidani (33.622725°N, 133.601904°E; elev. 139.3 m), 25 June 2021,

leg. TK, KUZ Z4067.

Additional materials. Japan: one adult and one juvenile, Honshu, Shizuoka, Fukuroi (34.739697°N, 137.977094°E; elev. 137.9 m), 22 March 2021, leg. TJ and TN, KUZ Z4068, KUZ Z4069; one adult, Shizuoka, Kakegawa (34.747118°E, 137.977556°E; elev. 98.4 m), 22 March 2021, leg. TJ, KUZ Z4070; one juvenile, Wakayama, Kinokawa (34.32959°N, 135.38936°E; elev. 401.2 m), 6 September 2019, leg. TN, KUZ Z4071; one male, Wakayama, Kushimoto (33.5195354°N, 135.7333847°E), 20 November 2021, leg. Ibuki Fukuyama (IF), KUZ Z4072; one male, Wakayama, Kushimoto (33.5218406°N, 135.7834739°E), 21 November 2021, leg. IF, KUZ Z4073; one female, Wakayama, Susami (33.5294052°N, 135.6116493°E), 21 November 2021, leg. Genki Nakatsu, KUZ Z4074; one adult and one juvenile, Tokushima, Ôkejima Island (34.209556°N, 134.618083°E; elev. 51.2 m), 8 June 2021, leg. Naoto Sawada (NS), KUZ Z4075, KUZ Z4076; one female, Shikoku, Ehime, Touon (33.726794°N, 132.902328°E; elev. 1037.4 m), 8 June 2021, leg. NS, KUZ Z4077; one male, Kochi, Agawa, Mt. Kanpuzan (33.79900726°N, 133.265461°E; elev. 1205.5 m), 24 July 2021, leg. Futaro Okuyama, KUZ Z4078.

Description. Body length of adults 48–60 mm in absolute ethanol (live specimens 55–67 mm). Body color brownish orange or dark red; antennae, legs, and ultimate legs brownish yellow (Fig. 2B).

Antennae approx. 0.2–0.21× as long as body, composed of 17 articles, density of setae increasing toward distal articles; basalmost article with sparse minute hairs and short setae dorsally; 2nd and subsequent articles setose, 3rd–17th articles more densely covered with setae (Fig. 3A). Cephalic plate as long as wide, sides converging anteriorly (Fig. 3B); its surface finely punctate; short lateral marginal sulci present in posterior half (Fig. 3B, C).

Second maxillae article 2 with elongated and semi-transparent dorsal spur distally; dorsal brush without transparent margin (Fig. 3D, E); pretarsus consisting of dark brown basal and semi-transparent short apical parts (Fig. 3D, E). Forcipular coxosternite and trochanteroprefemora sparsely punctate, coxosternite without sutures (Fig. 3F); forcipular trochanteroprefemur with small and blunt black process, with apparent basal suture (Fig. 3F); anterior margin of coxosternite darkly sclerotized, weakly rounded and slightly bilobed (Fig. 3F).

Tergites finely punctate; tergite 1 with anterior transverse suture, anterior margin covered by cephalic plate (Fig. 4A). Paramedian sutures present on tergites 2–22 (Fig. 4A); lateral marginations complete on tergites 6–21.

Sternites lacking sutures, finely punctate; sternites 2–20 with shallow longitudinal sulcus and transverse depression (Fig. 4B), both of them shallower and unapparent on anterior sternites. Sides of sternite 23 converging posteriorly, posterior margin slightly concave (Fig. 4C).

Spiracles ovoid, present on leg-bearing segments 3, 5, 8, 10, 12, 14, 16, 18, 20, and 22.

Legs lacking setae; tarsi of legs 1–21 undivided; legs 1–19 with lateral and ventral tibial spurs and tarsal spur; legs 20 and 21, respectively, with tibial spur and tarsal spur (or leg 21 with tarsal spur only); leg 22 without spurs. All legs with two accessory spines.

Coxopleuron approx. 1.5–1.7× as long as sternite 23

(Fig. 4D). Dorsal margin of ultimate pleuron protruding from lateral side of tergite 23 (Fig. 4E), posterior margin with minute dark spine (Fig. 4D). Posterior and ventral margins of coxopleuron converging posteriorly, forming approx. 60–65° angle (Fig. 4D); coxopleural process moderately long, tip of process pointed, slightly directed dorsally (Fig. 4D). Surface of coxopleuron without setae, covered with coxal pores of various size; coxopleural process and dorso-posterior area of coxopleuron poreless (Fig. 4D).

Ultimate leg 13.9–15.1 mm in length, 0.26–0.29× longer than body; all articles lacking setae (Fig. 5A); prefemur with two conical and pointed spinous processes, ventral process large, dorso-medial one minute; pretarsus with two short accessory spines.

Genital segment occupying approx. 1/2–2/3 length of sternite 23. Sternite of genital segment 1 with sparse minute setae; posterior margin weakly convex (Fig. 5B, C). Sternite of genital segment 2 well developed in males, covered with sparse minute setae; posterior part of genital segment 2 overlapped by anal valves, penis not visible in ventral view (Fig. 5B); genital segment 2 absent in females (Fig. 5C).

Remarks. No types were designated in the original description; Takakuwa (1937) mentioned, in German, that *S. elegans* was collected at Katsurahama, the southern coast of Kochi Prefecture, and Besshi in the northern area of Ehime Prefecture (“Sikoku [Katurahama, Bessji]”) but explicitly stated, in Japanese, that the description of *S. elegans* was based on several specimens collected from Katsurahama, and that he later found the same species in his specimens from Besshi. In accordance with Article 73.2.3 of the International Code of Zoological Nomenclature (hereinafter, Code; International Commission on Zoological Nomenclature, 1999), the type locality of this species is restricted to Katsurahama, Kochi. Takashima (1954) reported that two syntypes were preserved by the late Dr. Yasunori Miyosi, but we have not found these syntypes in his collection.

The syntypes of *S. elegans* seem to have been lost, but there is no doubt about the identity of this species, given the fact that no other species that bears the short cephalic marginal sulci and a longitudinal sulcus on sternites has been recorded from the type locality. Therefore, the nomenclatural status of this species does not meet the conditions of Article 75.1 of the Code; we thus do not designate a neotype for this species in the present study.

The studied material fits well with descriptions of Takakuwa (1937, 1940), except for the setae on the antennal articles and the marginations of tergites. While Takakuwa (1937, 1940) stated that all antennal articles were densely setose, all studied specimens bear the dorsal surface of the basalmost article covered with sparse hairs and setae, and subsequent articles densely covered with setae; thus, the description of the antennal features of *S. elegans* was amended in this study.

Takakuwa (1937, 1940) stated that *S. elegans* bears lateral margination on tergites 2–21 and 23, whereas the margination was complete on tergites 6–21 and 23 in our specimens. However, KUZ Z4064 has indefinite margination from tergite 3, so this character might be variable in *S. elegans*.

Takakuwa (1937) also mentioned that “23. Tergit seitlich ... schmalwulstig berandet, hinten in eine kleine Dornspitze endigend” (= 23rd tergite ... with narrow and pro-

truded margins, ending with a distal minute spine) and the same conditions were mentioned by Takakuwa (1940). However, the present examination revealed that “schmalwulstig berandet” (protruded margin) and “kleine Dornspitze” (distal process) occur on the dorsal and posterior margins of ultimate pleuron, respectively (Fig. 4D, E).

The number of tibial spurs on the legs of our specimens varied. KUZ Z4061 and KUZ Z4063, collected from the type locality, had two tibial spurs on legs 1–19, 1 tibial spur on leg 20, and no spurs on legs 21 and 22, which is consistent with Takakuwa’s (1937, 1940) observations, whereas a tibial spur was present on leg 21 of other individuals.

This species is quite similar to *S. curtus* but can be distinguished by the following characters: 2nd and subsequent antennal articles densely covered with short setae (vs. 4th and subsequent articles densely setose in *S. curtus*), presence of lateral short sulci on cephalic plate, rounded anterior margin of coxosternite (vs. virtually straight anterior margin; compare Fig. 3F and Fig. 7F), dorsal margin of ultimate pleuron protruding from the lateral margin of tergite 23 (vs. dorsal margin flattened, compare Fig. 4E and Fig. 8E), and moderately long coxopleural process (vs. short one, compare Fig. 4D and Fig. 8D). The density of setae on the basal antennal articles is known to be variable in some *Scolopocryptops* species (Shelly, 1992, 2002) but is treated here as a diagnostic character based on the consistency of the morphology of our specimens and previous observations of *S. curtus* (Takakuwa, 1939, 1940; Chao and Chang, 2008).

This species is absent in Bonato et al. (2016) and thus should be added to it, because *S. elegans* can receive a distinct taxonomic status.

Distribution. Honshu, Shikoku, and Kyushu (Takakuwa, 1939; Shinohara, 1950); abundant in Shikoku (Takashima and Shinohara, 1952). Also recorded from Miyakejima Island, Izu Islands (Takano, 1979), and Uotsuri Island, Senkaku Islands (Ikehara and Shimojima, 1971). The record from Iriomote Island, Ryukyu Islands (Ōmine et al., 1982) was possibly based on misidentified *S. curtus* specimens (see below).

***Scolopocryptops curtus* (Takakuwa, 1939)**

[Japanese name: Mijika-akamukade]

(Figs. 6–9)

Otocryptops curtus Takakuwa, 1939, pp. 698–700, figs. 1, 2, 4; Takakuwa, 1940, pp. 76–77, figs. 81, 82; Miyosi, 1971, p. 734.

Scolopocryptops curtus: Shinohara, 1978, p. 3; Chao and Chang, 2003, p. 4, fig. 20; Chao and Chang, 2008, pp. 2–3, figs. 1, 2; Shinohara et al., 2015, pp. 879, 905.

Amended diagnosis. Antenna with sparse minute hairs and short setae on basal three articles, 4th and subsequent articles densely setose. Cephalic plate without sulci or sutures. Forcipular coxosternite with anterior margin virtually straight, divided into two low lobes. Coxopleuron approx. 1.5× as long as sternite 23; pleural dorsal margin not protruding from lateral margin of tergite 23, posterior and ventral margins forming approx. 70–80° angle; coxopleural process short.

Material examined. Taiwan: one female, Miaoli, Shei-Pa

National Park (24.49952°N, 121.11195°E), 19 March 2019, leg. TN, KUZ Z4079; Japan: one juvenile, Okinawa, Iriomote Island (24.400755°N, 123.849153°E), 2 April 2021, leg. NS, KUZ Z4080; one female, Iriomote Island (24.363222°N, 123.766056°E), 14 October 2021, leg. IF, KUZ Z4081; one subadult, Iriomote Island (24.380406°N, 123.818303°E), 28 March 2022, leg. Ryobu Fukuyama, KUZ Z4141.

Description of adults (KUZ Z4079 and Z4081). Body length 35 mm (KUZ Z4079: in absolute ethanol) or 62 mm (KUZ Z4081: in absolute ethanol; 66 mm in life). Body color dark red; antennae, legs, and ultimate legs brownish yellow (Fig. 6).

Antennae approx. 0.23 or 0.27× as long as body, composed of 17 articles; basal 3 articles with sparse minute hairs and short setae; 4th and subsequent articles densely setose (Fig. 7A). Cephalic plate as long as wide, with sides converging anteriorly (Fig. 7B); its surface finely punctate (Fig. 7B, C); marginal sulcus absent (Fig. 7B).

Second maxillae article 2 with elongated and semi-transparent dorsal spur distally (Fig. 7D); dorsal brush without transparent margin (Fig. 7D, E); pretarsus consisting of dark brown basal and semi-transparent short apical parts (Fig. 7D, E). Surface of forcipular coxosternite and trochanteroprefemora sparsely punctate, coxosternite without sutures (Fig. 7F); trochanteroprefemur with small and blunt black process, with apparent basal suture (Fig. 7F); anterior margin of forcipular coxosternite virtually straight and darkly sclerotized, divided into two low lobes by median diastema (Fig. 7F).

Tergites finely punctate; tergite 1 with anterior transverse suture, anterior margin covered by cephalic plate (Fig. 8A). Paramedian sutures present on tergites 2–22 (Fig. 8A); lateral marginations complete on tergites 6–20 (21).

Sternites lacking sutures, finely punctate; sternites 2–20 with shallow longitudinal sulcus (Fig. 8B); sulcus shallower and not definite on anterior sternites. Sides of sternite 23 converging posteriorly, its posterior margin slightly concave



Fig. 6. *Scolopocryptops curtus* (Takakuwa, 1939), from Iriomote Island, Ryukyu Islands, KUZ Z4081, live specimen, dorsal view (left ultimate leg lost). Scale bar: 10 mm.

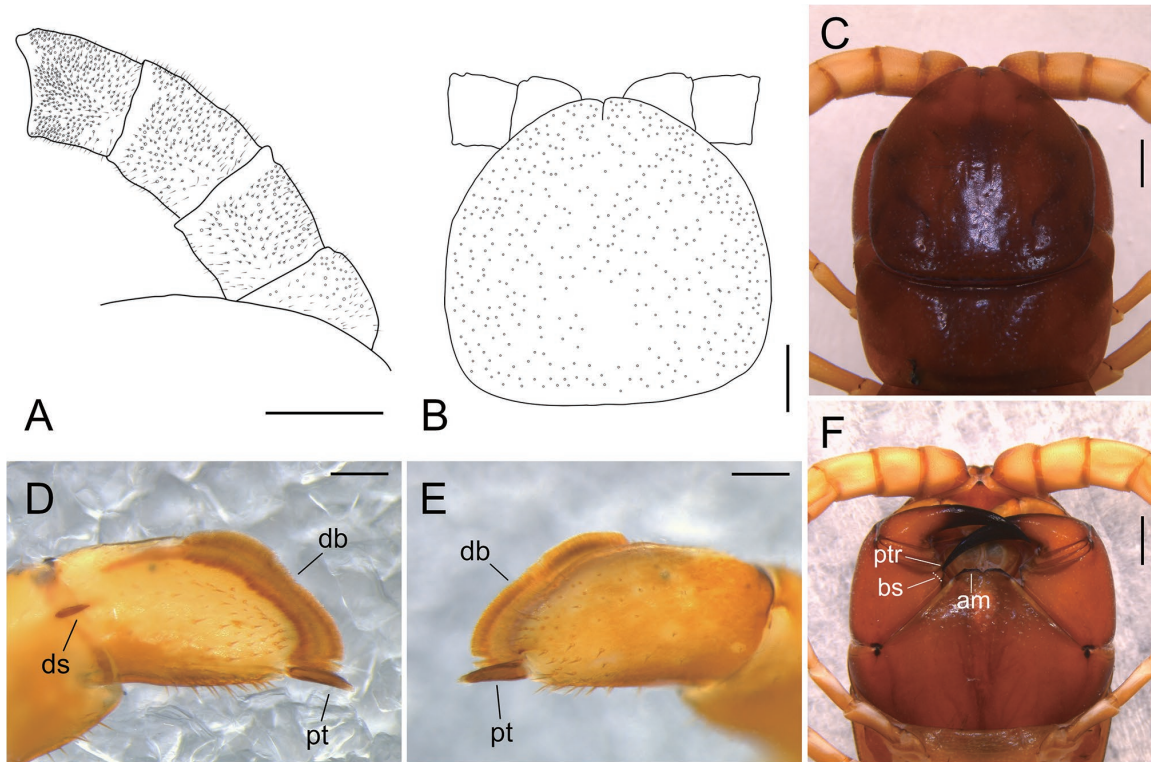


Fig. 7. *Scolopocryptops curtus* (Takakuwa, 1939), from Iriomote Island, Ryukyu Islands, KUZ Z4081. (A) Left antenna, dorsal view. (B) Cephalic plate, dorsal view. (C) Cephalic plate and tergite 1, dorsal view. (D) Distal part of article 2, article 3, and pretarsus of left second maxilla, medial view. (E) Article 3 and pretarsus of left second maxilla, lateral view. (F) Head, ventral view. Abbreviations: am, anterior margin of forcipular coxosternite; bs, basal suture on trochanteroprefemoral process; db, dorsal brush on article 3 of second maxilla; ds, dorsal spur on article 2 of second maxilla; pt, pretarsus of second maxilla; ptr, process of forcipular trochanteroprefemur. Scale bars: 1 mm (A–C, F); 0.2 mm (D, E).

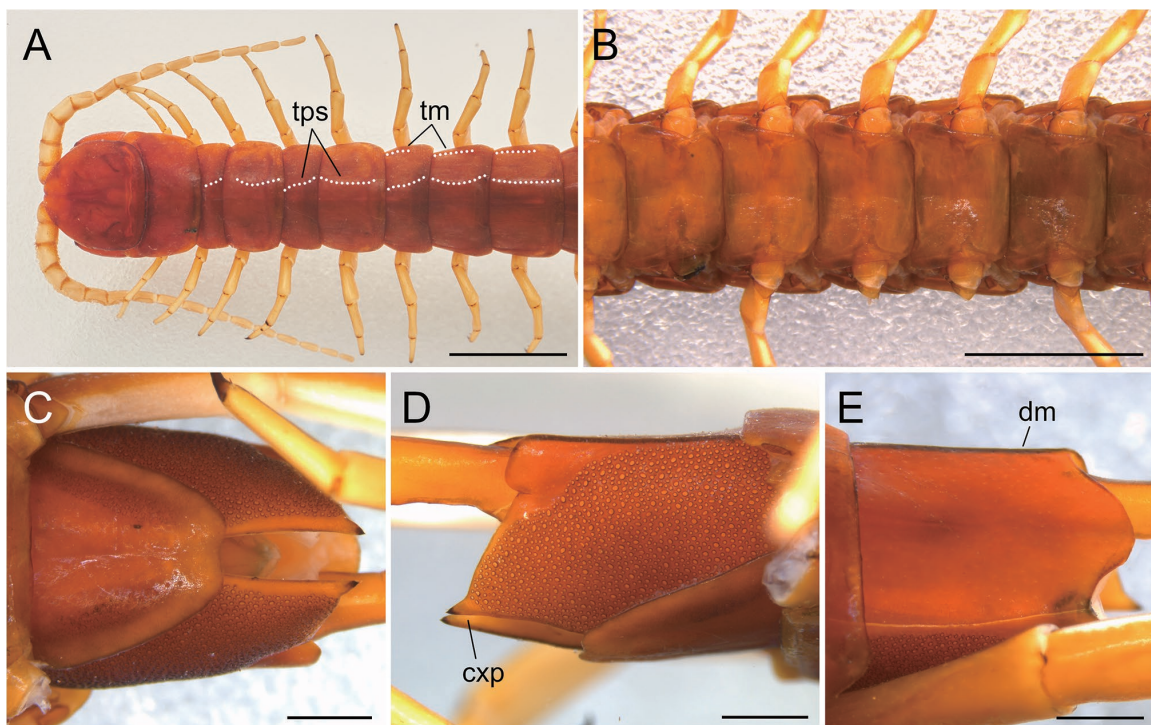


Fig. 8. *Scolopocryptops curtus* (Takakuwa, 1939), from Iriomote Island, Ryukyu Islands, KUZ Z4081. (A) Cephalic plate and tergites 1–8, dorsal view; dashed lines denote right tergal paramedian sutures and marginations. (B) Sternites 11–15, ventral view. (C) Sternite 23, ventral view. (D) Right coxopleuron, lateral view. (E) Tergite 23, dorso-lateral view. Abbreviations: cxp, coxopleural process; dm, dorsal margin of ultimate pleuron; tm, tergal margination; tps, tergal paramedian suture. Scale bars: 5 mm (A, B), 1 mm (C–E).

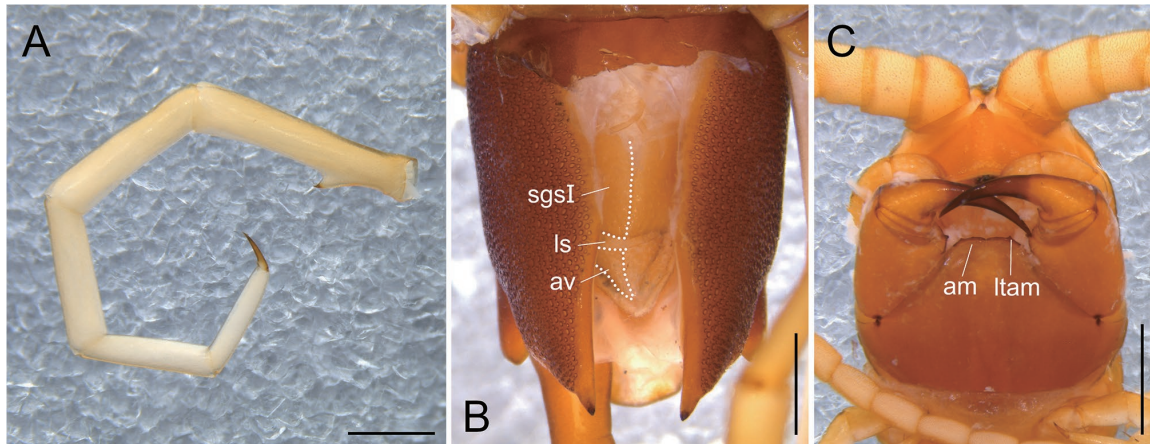


Fig. 9. *Scolopocryptops curtus* (Takakuwa, 1939), from Miaoli, Taiwan, and Iriomote Island, Ryukyu Islands, respectively, KUZ Z4079 (A), KUZ Z4080 (C), and KUZ Z4081 (B). (A) Right ultimate leg, lateral view. (B) Female genital segment, lamina subanalis, and anal valves, ventral view. (C) Head, ventral view. Abbreviations: am, anterior margin of forcipular coxosternite; av, anal valve; ls, lamina subanalis; ltam, lateral tooth on anterior margin of forcipular coxosternite; sgsI, sternite of genital segment 1. Scale bars: 1 mm.

(Fig. 8C).

Spiracles ovoid, present on leg-bearing segments 3, 5, 8, 10, 12, 14, 16, 18, 20, and 22.

Legs lacking setae; tarsi of legs 1–21 undivided. Legs 1–19 with lateral and ventral tibial spurs and tarsal spur; legs 20 and 21, respectively, with tibial spur and tarsal spur (or leg 21 with tarsal spur only); leg 22 without spurs. All legs with two accessory spines.

Coxopleuron approx. $1.5\times$ as long as sternite 23 (Fig. 8D). Dorsal margin of ultimate pleuron not protruding from lateral margin of tergite 23 (Fig. 8E), posterior margin with minute dark spine (only in KUZ Z4079). Posterior and ventral margins of coxopleuron converging posteriorly, forming approx. $70\text{--}80^\circ$ angle; coxopleural process short, tip of process pointed, slightly directed dorsally (Fig. 8D). Surface of coxopleuron without setae, covered with various sized coxal pores; coxopleural process and dorso-posterior area of coxopleuron poreless (Fig. 8D).

Ultimate leg 9.5 or 14.0 mm in length, 0.27 or 0.23 \times longer than body; all articles lacking setae (Fig. 9A); prefemur with two conical and pointed spinous processes, ventral process large, dorso-medial one minute; pretarsus with (or without) two accessory spines.

Genital segment occupying approx. $2/3$ length of sternite 23. Sternite of genital segment 1 sparsely covered with minute setae, posterior margin weakly convex (Fig. 9B). Lamina subanalis situated between genital segment and anal valves (Fig. 9B). Genital segment 2 absent in females (Fig. 9B).

Variation. Anterior margin of forcipular coxosternite with a pair of small lateral teeth in small specimens (KUZ Z4080 and Z4141, Fig. 9C).

Remarks. The original description of *S. curtus* was based on a single specimen collected from Hengchun Township, Pingtung County, Taiwan (“Kôsyun [Formosa]”), which is automatically fixed as the holotype. Takashima (1954) stated that the holotype was preserved by Dr. Yasunori Miyosi, but we could not find it in his collection. Therefore, the holotype of this species seems to have been lost, as has been already mentioned by Chao and Chang (2008).

The characteristics of our specimens are consistent with those described by Takakuwa (1939, 1940) and Chao and Chang (2008) except for body length: KUZ Z4081 was significantly larger (62 mm) than the specimens examined in those previous studies (25–50 mm).

Takakuwa (1939, 1940) described this species based on a specimen lacking most of legs; this specimen had two tibial spurs on leg 1, one tibial spur on legs 10–13, 2 tibial spurs on leg 19, and no spurs on legs 22 and 23. Chao and Chang (2008) subsequently noted that legs 1–19 bear two tibial spurs, and our specimens agree with their observation. Takakuwa (1939, 1940) also stated that legs 22 and 23 lack the accessory spines; the same character state was observed in the present specimen (KUZ Z4081). The lack of spurs and accessory spines possibly stem from the regeneration of legs, as mentioned by Lewis (2003) and Chao and Chang (2008). Additionally, Takakuwa (1939, 1940) and Chao and Chang (2008) described that *S. curtus* possesses a minute dark spine on the posterior margin of the ultimate pleuron. However, the spine was absent in one of our specimens (KUZ Z4081), and thus, this character might be variable in *S. curtus*.

Miyosi (1971) stated that this species has rudimentary cephalic marginal sulci, one of the diagnostic characters of *S. elegans*, while other features (e.g., setae on antenna and the shape of coxopleuron) were consistent with Takakuwa (1939). Miyosi also mentioned that *S. curtus* was known from southern Kyushu. Given that Ogawa (1961) recorded this species from Kagoshima Prefecture, southern Kyushu (see below) and indicated that the specimens were identified by Miyosi, Miyosi’s (1971) description was presumably based on Ogawa’s (1961) specimens. Materials from this locality need reexamination.

Distribution. Kagoshima Prefecture, Kyushu (Ogawa, 1961); Okinawa Island, Ishigaki Island, and Iriomote Island, Ryukyu Islands (Ômine, 1969; Ômine and Ito, 1998); and Taoyuan, Hsinchu, Chiayi, Kaohsiung, and Pingtung, Taiwan (Takakuwa, 1939; Chao and Chang, 2008). The records from Kyushu and Okinawa Island require reexamination (see Discussion).

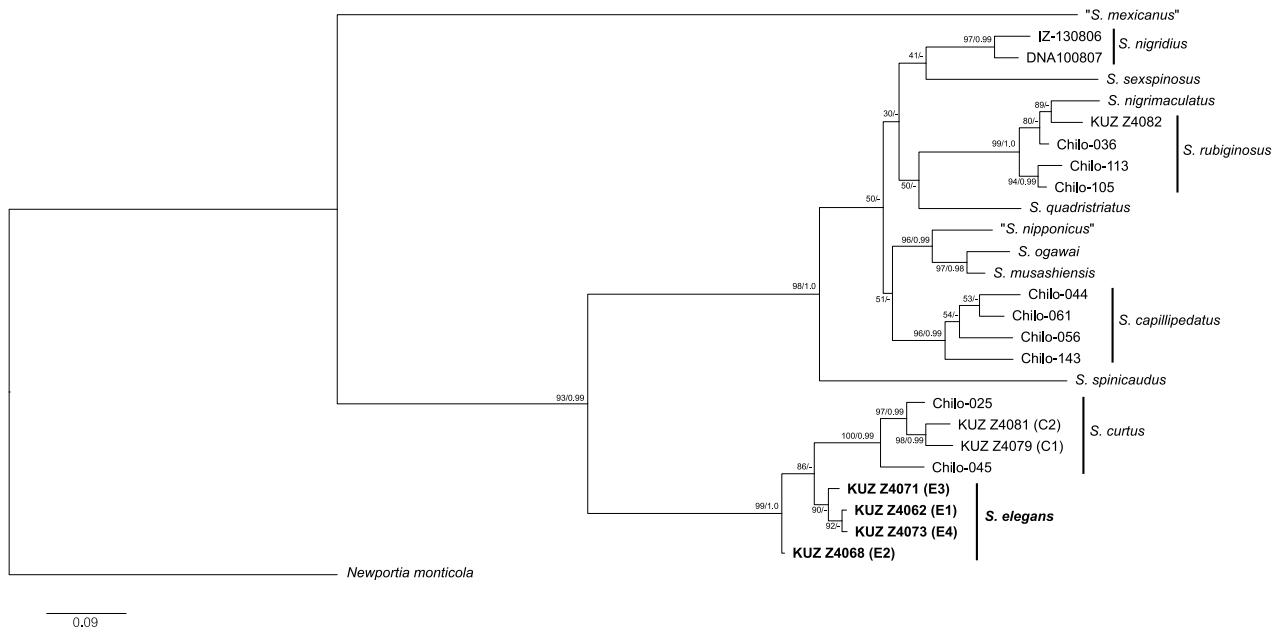


Fig. 10. Maximum likelihood tree ($\ln L = -6174.18$) for 1132 bp aligned positions of the 28S rRNA and COI sequences. Numbers on nodes indicate ML bootstrap values and Bayesian posterior probabilities. Locality numbers (E1–E4, C1, and C2) are shown in Fig. 1 and Table 1.

Molecular phylogenetic and genetic distance analyses

The ML ($\ln L = -6174.18$; Fig. 10) and BI (mean $\ln L = -6183.98$; not shown) trees showed nearly identical topologies. The monophyly of the “Asian/North American” group (sensu Vahtera et al., 2013) was well supported; within the “Asian/North American” clade, *S. elegans* and *S. curtus* comprised a monophyletic lineage with strong support (BS = 99%, BPP = 1.0). This clade was sister to the clade containing all other “Asian/North American” species (BS = 98%, BPP = 1.0). Within the (*S. elegans* + *S. curtus*) clade, the monophyly of *S. curtus* was well supported (BS = 100%, BPP = 0.99), whereas *S. elegans* was paraphyletic: KUZ Z4068, collected from Shizuoka (E2 in Figs. 1, 10 and Table 1), was separated from the other specimens comprising a monophyletic group (BS = 90%, BPP = 0.91). The AU test showed that there was no significant difference in the fit of a phylogeny in which the *S. elegans* specimens were constrained to be monophyletic and a phylogeny without this constraint ($P = 0.374$), indicating that the monophyly of *S. elegans* cannot be rejected.

The COI sequence divergence within KUZ Z4062, Z4071, and Z4073, which formed a monophyletic group, from Wakayama and Kochi ranged from 1.41% to 3.91%, and the sequence divergence between KUZ Z4068 from Shizuoka and this monophyletic group was 5.28–5.48%. Intraspecific variation in COI sequence divergence within *S. curtus* was 5.93–8.89%, and that between *S. elegans* and *S. curtus* was 9.2–12.1%.

DISCUSSION

The obtained phylogeny strongly supported the monophyly of *S. curtus* from Taiwan and Iriomote Island, while the specimens identified as *S. elegans* were paraphyletic. However, both ML and BI analyses failed to resolve the basal relationships of these specimens, and the hypothesis of monophyly of the “*S. elegans*” was not rejected by an AU

test. The COI divergence among the present “*S. elegans*” specimens fell within the intraspecific distances of *S. sexspinosus* and several *Scolopocryptops* species calculated by previous studies (Garrick et al., 2018) and were clearly smaller than the interspecific divergence between our specimens of “*S. elegans*” and *S. curtus*. Given that no significant morphological differences were observed among our specimens, all specimens from Honshu and Shikoku were treated as *S. elegans*.

The tree showed that *Scolopocryptops* species of the “Asian/North American” group consist of two main lineages: the clade comprising *S. elegans* and *S. curtus*, which are endemic to the Far Eastern islands, and the clade comprising all other “Asian/North American” species. *Scolopocryptops elegans* and *S. curtus* share similar morphological characters, viz., large body size, absence of complete marginal sulcus/sulci along the lateral margin of the cephalic plate, article 3 of the second maxilla lacking a transparent margin on the dorsal brush, and the presence of the sternal longitudinal sulci. These species are also similar in their reddish body color.

Most other “Asian/North American” *Scolopocryptops* bear the marginal sulcus/sulci on the cephalic plate, except the North American *S. peregrinator* (Crabill, 1952), *S. gracilis* Wood, 1862, and the Chinese *S. zhijiensis* Qiao et al., 2021 (the latter described based on an immature individual). It is also notable that transparent margin on the dorsal brush of the second maxilla can be recognized in the Neotropical species *S. melanostoma* Newport, 1844 and several species of *Newportia* Gervais, 1847, which is a sister group of *Scolopocryptops* (e.g., Chagas-Jr, 2018; Schileyko, 2018; Schileyko et al., 2020), and also in our specimens of “Asian/North American” *Scolopocryptops* species (i.e., *S. rubiginosus*, *S. quadristriatus*, *S. ogawai*, and *S. musashiensis*) (T. Jonishi, unpublished data). The absence of a transparent margin is possibly another character shared by *S. elegans*

and *S. curtus*. As this feature has not been described in many other species, a future study is needed to evaluate whether the absence of the transparent margin is a synapomorphy between *S. elegans* and *S. curtus*.

The distributions of *S. elegans* and *S. curtus* require further investigations. The southernmost record of *S. elegans* is from Iriomote Island, Ryukyu Islands, and *S. curtus* has been reported from southern Kyushu (Ogawa, 1961; Ômine et al., 1982), indicating that the ranges of these two species exhibit wide overlap from southern Kyushu to the southern Ryukyu Islands. However, our morphological and molecular findings demonstrated that the specimens from Iriomote Island belong to *S. curtus*. Because of their morphological similarities, these two species have possibly been misidentified in previous studies. Further faunal surveys and taxonomic studies are needed to elucidate the true ranges of *S. elegans* and *S. curtus* in the Japanese Archipelago, the Ryukyu Islands, and Taiwan.

Our phylogenies also suggested that the taxonomic accounts of several Asian and North American *Scolopocryptops* species should be revisited. *Scolopocryptops nipponicus*, described from eastern Honshu, was synonymized with North American *S. spinicaudus* by Shelly (2002). However, "*S. nipponicus*" was deeply divergent from *S. spinicaudus* in the tree, as mentioned in Edgecombe et al. (2012), and formed a clade with the Japanese *S. ogawai* and *S. musashiensis*. These three species are distinguishable by the density of the setae on ultimate legs, but the COI genetic distances between our specimens were low (5.88–9.54%) compared with levels of interspecific divergence in our dataset. Close relationships between the Chinese species *S. nigrimaculatus* and *S. rubiginosus* from Japan, China, Taiwan, and Vietnam, are also notable, given the COI genetic distance between *S. nigrimaculatus* and *S. rubiginosus* (5.96–8.87%) and the "intraspecific" divergence within *S. rubiginosus* (2.6–6.97%). Additional systematic study is needed to clarify the diversity and phylogeny of the "Asian/North American" *Scolopocryptops* centipedes.

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COMPETING INTERESTS

The authors have no competing interests to declare.

AUTHOR CONTRIBUTIONS

TJ conceived the study and conducted morphological observations and molecular experiments. TJ and TN wrote the manuscript, and prepared figures.

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